A RHAETO-LIASSIC FLORA FROM AIREL, NORTHERN FRANCE

by M. MUIR and J. H. A. van KONIJNENBURG-van CITTERT

ABSTRACT. An assemblage of fossil plants from the Upper Triassic/Liassic of Airel (Manche), Northern France, is recorded, and two new species, *Hinnerella airelensis* sp. nov. and *Classopollis harrisii* sp. nov., are described and figured. *In situ* and dispersed pollen is compared and a lycopod megaspore and microspore described. The assemblage is compared with others from France and Wales.

THE plant material described in this paper was recovered from some sandy, light-grey clay collected from Airel in the Carentan basin, near Caen, France. Various suggestions have been made about the age of the deposit (Larsonneur 1962, 1963) ranging from Norian to Hettangian. The assemblage is limited, but is generally comparable with the assemblages described by Levet-Carette (1964) and Briche, Danzé-Corsin, and Laveine (1963) from deposits in the neighbourhood of the Boulonnais. Their material came from fissure-fillings in the Carboniferous, while our material appears to be lacustrine, the plants being associated with ostracods and charophytes (Larsonneur 1963).

The macrofossils are in a remarkably good state of preservation; they are almost uncompressed, and the spiral leaf arrangement is evident. Leafy shoots, fragments of leaves, female cone-scales, male cone axes, fragments of microsporophylls, and separate pollen masses were recovered and are here described. Dispersed megaspores, microspores, and pollen from the clay were also examined.

Methods of study. Selected macrofossils were treated by maceration in Schulze's solution followed by dilute ammonia. The male cone fragments were recovered by bulk maceration of the clay, which was disintegrated in water, and then treated with Schulze's solution. Specimens were then mounted in glycerine, and examined and photographed with a Leitz Ortholux microscope. Some of the macrofossil cuticles, pollen masses, and megaspores (both macerated and unmacerated) were mounted on Durofix, coated with gold/palladium and examined on a Cambridge Instrument Company 'Stereoscan' scanning electron microscope.

The microfossils were recovered by a standard method, i.e. disintegration of the clay in H_2O_2 , followed by HCl, HF, and HCl treatment. The residue was then macerated in concentrated nitric acid and washed in distilled water. The microspores were then mounted in glycerine jelly and examined and photographed in a Zeiss photomicroscope.

SYSTEMATIC DESCRIPTIONS

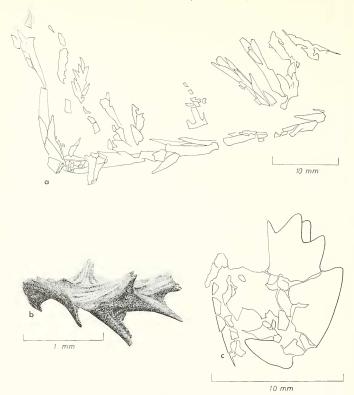
Genus HIRMERELLA Hoerhammer emend. Jung

Type species, H, (Cheirolepis) muensteri (Hoerhammer) Jung.

Hirmerella airelensis sp. nov.

Plate 78, figs. 1-5; Plate 79, fig. 2; Plate 80, fig. 1; text-fig. 1A

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TEXT-FIG. 1. Hirmerella airelensis sp. nov. a, Holotype; $\times 2.5$. b, Isolated male cone axis; $\times 30$. c, Partly broken female cone scale, $\times 5$.

Holotype. Specimen 2845: division of Palaeobotany and Pollen-morphology, Museum and Herbarium of the State University of Utrecht.

Diagnosis. Leaves spirally arranged; rather variable; free part 2–5 mm. long, 2–4 mm. wide, leaf-base cushion 2–3 mm. long, 2–4 mm. wide. Cuticle from 1 to 8 μ thick, usually about 4–6 μ ; margin scarious, especially near the apex. Upper cuticle: stomata mostly arranged in short longitudinal rows, but some irregularly scattered; rows separated laterally by 3–10 epidermal cells in thin cuticles, 2–6 in thick ones; stomata within rows separated longitudinally by 2–10 epidermal cells in thin cuticles, 1–6 in

thick ones; guard cells sunken, not usually visible; 4–6 subsidiary cells forming a thick, raised ring around the guard cells, often striated and, especially in the thick cuticles, papillate; encircling cells present but not clear; normal epidermal cells in rows, papilate, varying from rectangular with thin walls, to almost square with thick walls; thick walls often pitted. Lower cuticle similar to the upper, but with more stomata, and with few papillae on the epidermal cells.

Description. The material consists of a large number of well-preserved small shoots, usually not more than 2 cm. long. Most of the material is uncompressed and shows the spiral arrangement of the leaves very well.

The leaves vary considerably in size and proportions, from rather long narrow ones, with a large free part, and a rather thin cuticle, to broader ones with a short free part and a rather thick cuticle. All kinds of intermediates between these two extremes have been found. We believe that the long narrow leaves are immature, whilst the broader ones are older, although they may represent sun and shade leaves. It is known that the young and old leaves of recent conifers commonly differ considerably in cuticle thickness and size of the epidermal cells (Napp-Zinn 1966). We very often find *Classopollis harrisii* sp. nov. pollen grains sticking to the thicker cuticles, which reinforces our opinion that they are older leaves.

Discussion and comparison. These shoots can certainly be placed within the genus Hirmerella, but they differ in some respects from the type species Hirmerella muensteri.

In *H. muensteri*, the cells of the upper cuticle do not have papillae, while in our species, these are prominent. There are more, and longer, rows of stomata, and the stomata are more closely crowded together within rows in *H. muensteri* than *H. airelensis* (Plate 78, fig. 6); the stomata appear to be indistinguishable in the two species.

The presence of male and female cone-scales and of pollen grains which resemble those of *H. nuensteri* confirm the placing of the new species within the genus *Hirmerella*.

This material resembles very closely that described by Lewarne and Pallot (1957) and Harris (1957) from the Rhaeto-Liassic of Cnap Twt, South Wales, although these authors did not mention papillae on the upper cuticle, but thickenings. Re-examination of the material shows the 'central thickenings' to be papillae, and the stomata are rather widely spaced in short rows. Although the Welsh material agrees more in morphology with our species, it was referred to *Cheirolepis* (now *Hirmerella*) muensteri. Lemoigne (1967) has described some leafy shoots from Saint Fromond (Manche) in the same region of the Carentan Basin as Airel. Although they were referred to the 'Cupressales', in their over-all morphology and cuticular detail, they appear to be identical with our material. The stomata are very similar, and papillae are present as well. There seems to be no basis for their assignation to the 'Cupressales', and we believe that they should be placed in *Hirmerella airelensis* sp. nov.

Our material is closely comparable with that described by Chaloner (1962) from the Henfield borehole. He found that the isolated leaves are similar in all respects with those from Cnap Twt described by Lewarne and Pallot (1957) and Harris (1957). He mentions the papillae on the epidermal cells, but refers his material to *Cheirolepis muensteri*. We believe that these leaves, although fragmentary could be referred to *Himperella airclensis*.

Wood (1961) describes *Cheirolepis muensteri* from Lyme Regis, Dorset, England. While his material is similar to ours, it differs in having very thick cuticles (15–20 μ) and not showing papillae on the walls of the epidermal cells.

Isolated female cone-scales. About ten isolated female cone-scales were found (textfig. 1c). Among them are a few isolated bract scales which yield good cuticles. The cuticles are like those of *Hirmerella muensteri* as described by Hirmer and Hoerhammer (1934) except that they show papillae on the upper (outer) sides of the cells, which are the same as those occurring on the vegetative shoots.

Some ovuliferous scales were found too, showing a clear five-fold division (see text-fig. 1c). In one case, a six-fold division was observed, the middle appendage being split. No complete seeds were discovered, but one megaspore membrane (7 mm. long) was found in a bulk maceration.

The female cone-scales agree closely with those of *Hirmerella muensteri* except for the papillae on the cuticle of the bract scale, and demonstrate that this new fossil conifer must be placed within the genus *Hirmerella*. Harris (1957) stated that he had found female cone-scales like those of *Hirmerella muensteri*, but he does not give any description or drawing. There are no preparations of female cone-scales in his material kept at

EXPLANATION OF PLATE 78

All transmitted light photographs of macerated cuticles.

Figs. 1–5. *Hirmerella airelensis* sp. nov. 1, Upper cuticle, showing papillae in the cells; ×250. 2, Thin lower cuticle, showing stomata; ×250. 3, Stoma, showing striations on the subsidiary cells; ×750. 4, Detail of epidermal cells showing pitting of walls; ×750. 5, Cell outlines and stomatal arrangement at edge of upper and lower cuticle; ×250.

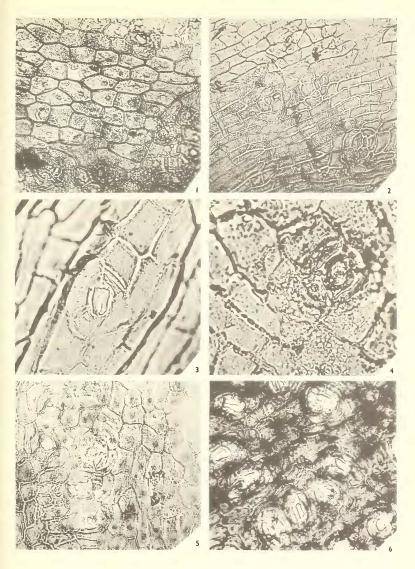
Fig. 6. Hirmerella muensteri (Schenk) Jung. Cell outlines and arrangement of stomata, for comparison with fig. 5; note absence of papillae; ×250.

EXPLANATION OF PLATE 79

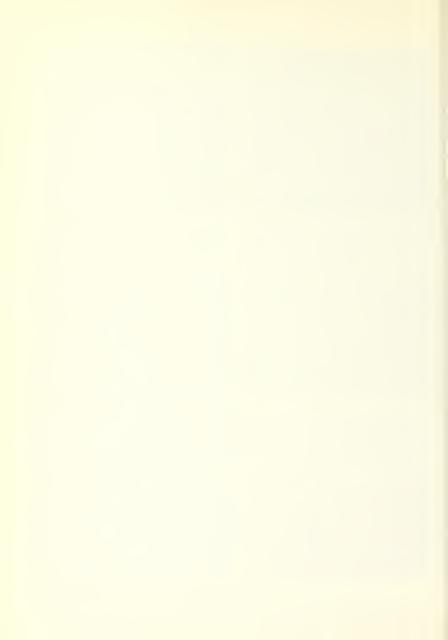
- Figs. 1, 3. Stereoscan photographs of pollen mass of *Classopollis harrisii* sp. nov. 1, General morphology of the whole mass; ×300. 3, Morphology of single grain (centre), with series of pustules on surface representing collapse of outer surface of wall over the coarse bacula; ×1500.
- Fig. 2. Stereoscan photograph of edge of cuticle of *Hirmerella airelensis* sp. nov., showing the papillae, and three stomata arranged in a row; ×250.
- Fig. 4. Pollen mass of Classopollis harrisii sp. nov. showing an immature grain with a thin wall and tetrad mark; ×1000.
- Figs. 5–8. Classopollis harrisii sp. nov.; ×1000. 5. Very immature grain showing prominent triradiate mark, and weakly developed wall structure. 6, Smooth inner body, isolated by pressing the cover slip. 7, Co-type of dispersed pollen species, showing all general features. 8, Holotype of dispersed pollen species, showing coarse baculae clearly.

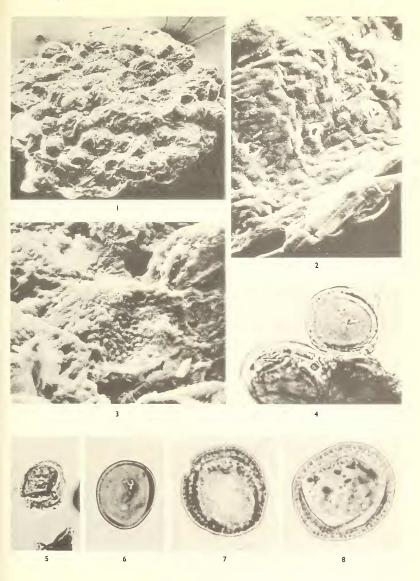
EXPLANATION OF PLATE 80

- Fig. 1. Hirmerella airelensis sp. nov., slightly compressed shoot showing leaf arrangement; Stereoscan photograph, ×25.
- Fig. 2–5. Bacutriletes tylotus (Harris) Potonié. 2, Stereoscan photograph showing the general morphology and triradiate mark; ×200. 3, Transmitted light photograph of B.M. specimen V 32623 of Lewarne and Pallot, for comparison with fig. 2; ×200. 4, Detail of fig. 2; ×400. 5, Detail of fig. 3; ×400.
- Figs. 6, 7. Heliosporites reissingeri (Harris) Chaloner 1969. 6, Detail of spine and surface; ×1000. 7, whole grain; ×600.

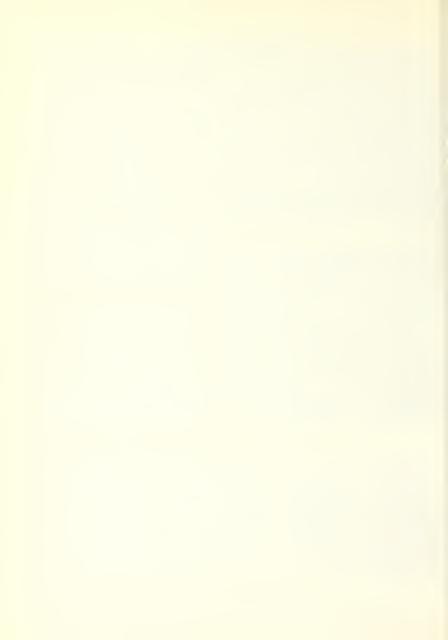


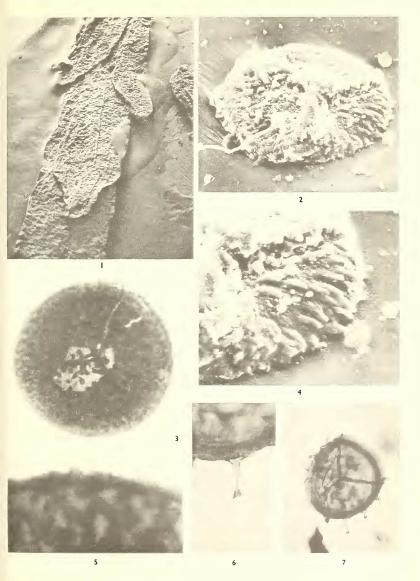
MUIR and VAN KONIJNENBURG VAN CITTERT, Mesozoic conifer cuticles





MUIR and VAN KONIJNENBURG VAN CITTERT, Mesozoic conifer pollen





MUIR and VAN KONIJNENBURG VAN CITTERT, Mesozoic conifer and spores

